

Variation in growth stimulation by elevated carbon dioxide in seedlings of some C₃ crop and weed species

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Abstract

Seven C₃ crop and three C₃ weed species were grown from seed at 360 and at 700 cm³ m^{−3} carbon dioxide concentrations in a controlled environment chamber to compare dry mass, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) and photosynthetic acclimation at ambient and elevated carbon dioxide. The dry mass at the final harvest at elevated carbon dioxide relative to that at ambient carbon dioxide was highly correlated with the RGR at the lower carbon dioxide concentration. This relationship could be quite common, because it does not require that species differ in the response of RGR or photosynthesis to elevated carbon dioxide, and holds even when species differ moderately in these responses. RGR was also measured for a limited period at the end of the experiment to determine relationships with leaf gas exchange measured at this time. Relative increases in RGR at elevated carbon dioxide at this time were more highly correlated with the relative increase in NAR at elevated carbon dioxide than with the response of LAR. The amount of acclimation of photosynthesis was a good predictor of the relative increase in NAR at elevated carbon dioxide, and the long-term increase in photosynthesis in the growth environment. No differences between crops and weeds or between cool and warm climate species were found in the responses of growth or photosynthetic acclimation to elevated carbon dioxide.

Keywords: acclimation, carbon dioxide, growth, photosynthesis, net assimilation rate, relative growth rate

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Introduction

The relative stimulation of plant growth by elevated carbon dioxide concentration varies greatly among plant species (Hunt *et al.* 1991, 1993; Poorter 1993), and may have important consequences for competition as the carbon dioxide concentration in the atmosphere changes. Except for the C₃–C₄ comparison, reasons for differences in growth stimulation have not been clear. The papers by Hunt *et al.* (1991, 1993), and Poorter (1993) point towards adaptive strategy and maximum growth rate as important factors affecting the growth stimulation by elevated carbon dioxide. The data presented by Hunt *et al.* (1991, 1993) consists primarily of the relative stimulation in biomass after about 50 days. The 'competitive' species, characterized by high potential relative growth rates (RGR), had the largest relative stimulation in biomass. This relationship could occur even if the percentage stimulation of RGR were the same across species (Poorter

1993). In that case the relative stimulation in biomass would be positively related to the RGR at ambient carbon dioxide. While this effect may not have caused the pattern observed by Hunt *et al.* (Hunt, personal communication), it needs to be considered in comparisons of biomass and growth rate. Poorter (1993) found substantial variation in the relative increase in RGR at elevated carbon dioxide among 10 wild species, and found that the relative stimulation in RGR tended to be greater in species with higher RGR in ambient carbon dioxide. There were no differences in the relative stimulation of photosynthesis by elevated carbon dioxide among the species in his study, suggesting that differences in the response of leaf area ratio (LAR) rather than net assimilation rate (NAR) determined how much RGR responded to elevated carbon dioxide, although this was not formally analysed. Others, however, have also found large differences among species in the amount of acclimation of photosynthesis to elevated carbon dioxide (Sage *et al.* 1989), which should result in

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Species	Mass (g)	RGR (g g ⁻¹ d ⁻¹)	Mass (elevated/ambient)	RGR
<i>Hordeum vulgare</i>	1.52	0.19	1.48	1.09
<i>Vicia faba</i>	3.08	0.10	1.30	1.11
<i>Pisum sativum</i>	1.57	0.12	1.39	1.12
<i>Brassica rapa</i>	2.20	0.31	2.26	1.11
<i>Glycine max</i>	3.72	0.13	1.55	1.14
<i>Lycopersicon esculentum</i>	3.39	0.27	1.78	1.09
<i>Solanum melongena</i>	1.73	0.25	1.88	1.13
<i>Chenopodium album</i>	1.60	0.22	1.56	1.08
<i>Abutilon theophrasti</i>	4.26	0.19	1.65	1.11
<i>Datura stramonium</i>	5.16	0.19	1.72	1.12
overall mean:		0.20	1.66	1.11
all crops:		0.19	1.66	1.11
all weeds:		0.20	1.64	1.10
cool climate species:		0.18	1.60	1.10
warm climate species:		0.21	1.72	1.12

Table 1 Final mass, relative growth rate (RGR) over the whole growth period, and the stimulation of final mass and RGR by elevated carbon dioxide of 10 species grown at 360 cm³ m⁻³ and 700 cm³ m⁻³ carbon dioxide concentrations

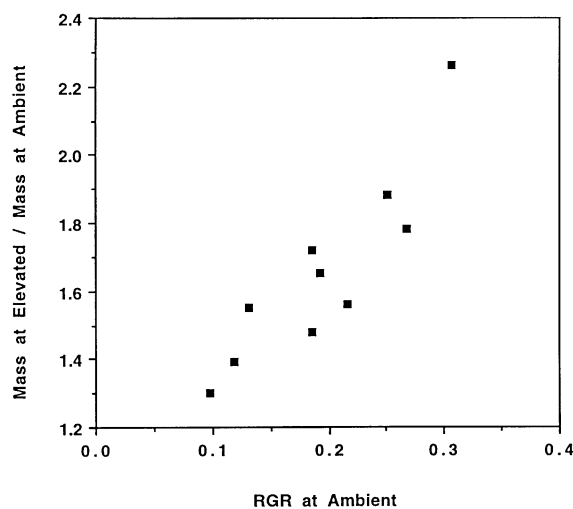


Fig. 1 Final dry mass of plants grown at 700 cm³ m⁻³ carbon dioxide concentration relative to the mass of plants grown at 360 cm³ m⁻³ as a function of the relative growth rate (RGR) for the whole growth period at the lower carbon dioxide concentration. The correlation coefficient was +0.897, and the probability was 0.0004.

differences in the stimulation of NAR. Furthermore, if photosynthetic acclimation can result from feedback inhibition of photosynthesis, then the increase in NAR and the decrease in LAR at elevated carbon dioxide might be correlated, because accumulation of carbohydrates tends to lower LAR. However, the correlation could conceivably be either positive or negative (Mauney *et al.* 1979). That is, a large increase in NAR could reduce LAR by carbohydrate accumulation, or a large increase in carbohydrates could reduce NAR by feedback inhibition of photosynthesis.

The purpose of the present work was to compare species in the same experiment for the relative stimulation

of biomass and RGR and the resolution of RGR into LAR and NAR, and the amount of leaf photosynthetic acclimation in response to a doubling of the current atmospheric concentration of carbon dioxide. RGR was determined for the whole growth interval, and also for six days at the end of the growth period when it was possible to measure leaf gas exchange for comparison with NAR. Seven C₃ crop species and three local C₃ weed species were compared, representing species adapted to both warm and cool climates.

Materials and methods

Crop species used were barley (*Hordeum vulgare* L. cv. Brant), broadbean (*Vicia faba* L.), eggplant (*Solanum melongena* L. cv. Early Beauty), pea (*Pisum sativum* L. cv. Maestro), soybean (*Glycine max* L. Merr. cv. Kent), tomato (*Lycopersicon esculentum* Mill. cv. Rutgers), and turnip (*Brassica rapa* L. cv. Purple Globe). The weeds studied were *Abutilon theophrasti* M., *Chenopodium album* L. and *Datura stramonium* L. Vegetable seeds were obtained from Burpee Seeds, Warminster PA. Seeds of barley and soybean and the weeds were obtained locally. Barley, broadbean, pea, turnip and *Chenopodium album* were considered cool climate species, based on our observations of higher RGR at 17 °C than at 30 °C in these species, but not in the others (data not shown).

All species were grown in one controlled environment chamber with successive runs at two carbon dioxide concentrations. The day/night air temperature was 26 ± 0.3/20 ± 0.3 °C, the dew point temperature was 18 ± 2 °C, and there was 500 µmol m⁻² s⁻¹ of photosynthetic photon flux density for 14 h per day provided by 'cool-white' fluorescent lamps. The carbon dioxide concentration of the chamber air was maintained at either

Table 2 Stimulation of relative growth rate (RGR), net assimilation rate (NAR) and net carbon dioxide exchange rate (NCE) at the growth PPFD of 10 species grown at 700 cm³ m⁻³ carbon dioxide concentration compared with plants grown at 360 cm³ m⁻³, and the amount of acclimation of photosynthesis measured at the growth PPFD for the interval of 18–24 d after emergence. Values in parentheses are absolute values for the ambient carbon dioxide treatment. Units are g g⁻¹ d⁻¹ for RGR, g m⁻² d⁻¹ for NAR, and μmol m⁻² s⁻¹ for NCE.

Species	RGR	NAR (elevated/ambient)	NCE	Acclimation (μmol m ⁻² s ⁻¹)
<i>Hordeum vulgare</i>	1.24 (0.25)	1.37 (13.9)	1.40 (15.0)	0.5
<i>Vicia faba</i>	0.86 (0.21)	1.03 (10.6)	1.36 (16.2)	2.6
<i>Pisum sativum</i>	0.95 (0.21)	1.08 (12.3)	1.37 (15.8)	2.9
<i>Brassica rapa</i>	0.94 (0.35)	1.07 (15.5)	1.32 (16.2)	2.6
<i>Glycine max</i>	0.96 (0.32)	1.10 (11.4)	1.36 (16.2)	2.0
<i>Lycopersicon esculentum</i>	1.03 (0.32)	1.33 (14.7)	1.41 (16.7)	0.0
<i>Solanum melongena</i>	0.97 (0.31)	1.30 (14.4)	1.38 (15.1)	1.5
<i>Chenopodium album</i>	0.93 (0.27)	1.10 (16.2)	1.30 (20.6)	2.8
<i>Abutilon theophrasti</i>	0.88 (0.24)	1.20 (15.7)	1.34 (18.4)	1.8
<i>Datura stramonium</i>	1.26 (0.25)	1.35 (15.2)	1.39 (18.8)	1.4
overall mean:	1.00	1.19	1.36	1.8
all crops:	0.99	1.18	1.37	1.7
all weeds:	1.02	1.22	1.34	2.0
cool climate species:	0.98	1.13	1.36	2.3
warm climate species	1.02	1.26	1.38	1.3

Table 3 Correlation coefficients (*r*) among the relative growth rate (RGR), and the relative stimulation of RGR, net assimilation rate (NAR) and leaf area ratio (LAR) by growth at 700 (elevated) compared to 360 cm³ m⁻³ (ambient) carbon dioxide concentration for 10 species for the interval of 18–24 d after emergence

Variable 1	Variable 2	<i>r</i>	Probability
RGR (elevated/ambient)	RGR (ambient)	0.013	0.973
RGR (elevated/ambient)	LAR (elevated/ambient)	0.567	0.087
NAR (elevated/ambient)	LAR (elevated/ambient)	-0.058	0.873

360 ± 50 or 700 ± 50 cm³ m⁻³ by injecting either pure carbon dioxide or carbon dioxide-free air under the control of an absolute infrared carbon dioxide analyser which sampled chamber air continuously. Plants were grown from seed one per pot in 15 cm diameter plastic pots filled with 1.8 dm³ of vermiculite and flushed daily with a complete nutrient solution.

Each experiment consisted of 10 plants of each species. For each species, two harvests of five plants each were made at 18 and 24 days from seed emergence. Between the harvests, leaf gas exchange was measured on five individuals per species. Two experiments were done at the ambient carbon dioxide concentration, and two at the elevated concentration, and combined data are presented. The initial harvest time was chosen so that the leaf chosen for gas exchange measurement reached its maximum photosynthetic capacity between the harvests. Leaf numbers chosen for gas exchange measurement were Leaf 2 in barley, eggplant and soybean, Leaf 3 in broadbean, *Datura*, tomato and turnip, Leaf 4 in *Abutilon* and pea,

and Leaf 6 in *Chenopodium*. These leaves were not shaded by other leaves between the two harvest times. At harvest, total leaf area was determined with a Li-Cor leaf area meter (Li-Cor Inc., Lincoln Nebraska), and leaf, stem and root dry mass were determined after drying at 65 °C. Relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) were calculated for the 18–24 day interval. RGR was also calculated for the whole 24 d growth period, using seed dry mass as the initial mass.

Steady-state rates of carbon dioxide and water vapour exchange of intact leaves were measured about 2 h after the lights came on at the growth conditions of photon flux, temperature, dew point temperature, and carbon dioxide concentration, using a CIRAS portable photosynthesis system (PP Systems). After measurement of plants grown at the lower carbon dioxide concentration at the growth carbon dioxide concentration, the carbon dioxide concentration around the measured leaf was switched to 700 cm³ m⁻³, and the steady-state net rate of carbon dioxide exchange (NCE) determined. The amount of

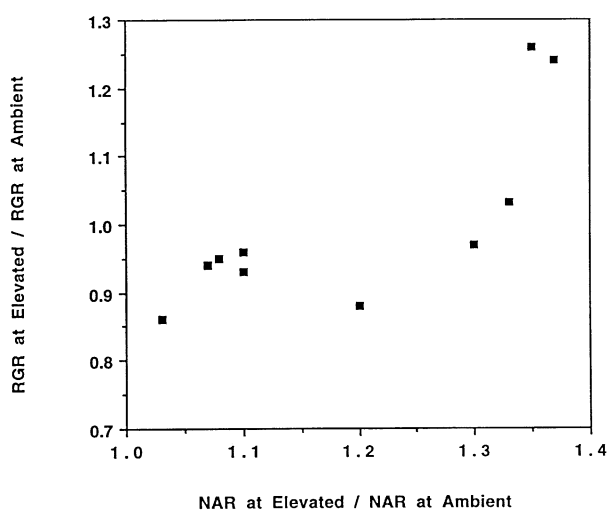


Fig. 2 Relative growth rate (RGR) for days 18 through 24 of plants grown at $700 \text{ cm}^3 \text{ m}^{-3}$ carbon dioxide concentration relative to that of plants grown at $360 \text{ cm}^3 \text{ m}^{-3}$ as a function of the values of net assimilation rate (NAR) at the higher relative to the lower carbon dioxide concentration. The correlation coefficient was $+0.782$, and the probability was 0.0076 .

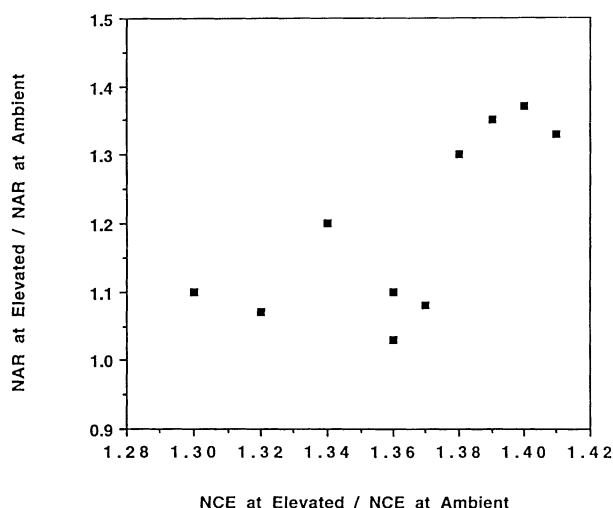


Fig. 3 Net assimilation rate (NAR) of plants grown at $700 \text{ cm}^3 \text{ m}^{-3}$ carbon dioxide concentration relative to that of plants grown at $360 \text{ cm}^3 \text{ m}^{-3}$ as a function of the value of net carbon dioxide fixation (NCE) in the growth conditions at the higher relative to the lower concentration. The correlation coefficient was $+0.719$, and the probability was 0.0190 .

photosynthetic acclimation was quantified as the difference in NCE at elevated carbon dioxide between acclimated and unacclimated leaves. These measurements were also repeated at a PPFD of $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ to determine the relationship between photosynthetic response measured at the growth PPFD and at high PPFD.

Linear contrasts were used to compare the responses of the crop and weed species, and the cool climate and warm climate species.

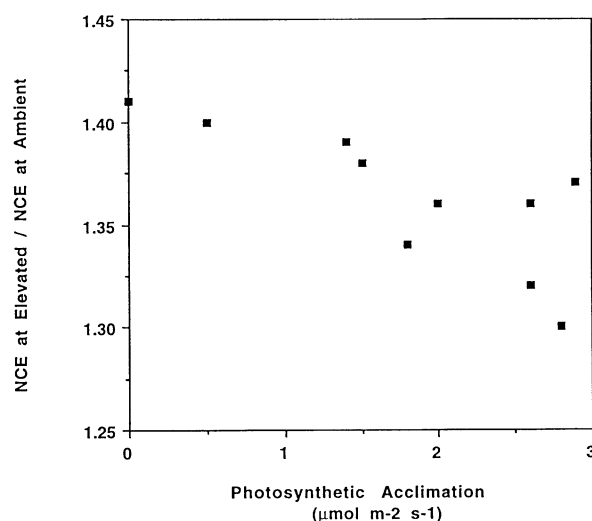


Fig. 4 Net carbon dioxide fixation rate (NCE) in the growth conditions at $700 \text{ cm}^3 \text{ m}^{-3}$ carbon dioxide concentration relative to that at $360 \text{ cm}^3 \text{ m}^{-3}$ as a function of amount of acclimation of photosynthesis measured at the growth PPFD. The correlation coefficient was -0.779 , and the probability was 0.0079 .

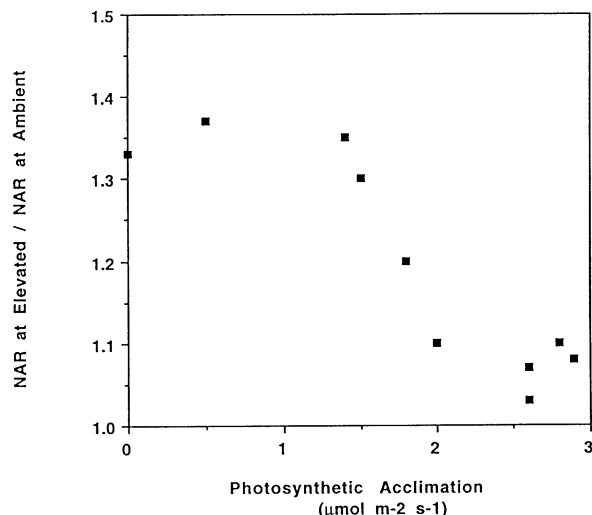


Fig. 5 Net assimilation rate (NAR) of plants grown at $700 \text{ cm}^3 \text{ m}^{-3}$ carbon dioxide concentration relative to that of plants grown at $360 \text{ cm}^3 \text{ m}^{-3}$ as a function of the amount of acclimation of photosynthesis measured at the growth PPFD. The correlation coefficient was -0.883 , and the probability was 0.0007 .

Results

Dry mass at the final harvest was increased by factors of 1.30 – 2.26 at the elevated carbon dioxide concentration, with a mean factor of 1.66 (Table 1). The stimulation in final mass by elevated carbon dioxide was highly correlated with RGR at the lower carbon dioxide concentration (Fig. 1). There was no significant correlation between the stimulation in the final mass and the relative

Table 4 Correlation coefficients (r) between the net long-term stimulation of net carbon dioxide exchange rate (NCE) at the growth carbon dioxide concentrations measured at the growth PPFD (500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and the amount of acclimation of photosynthesis to elevated carbon dioxide measured at the two PPFDs. Ten species were grown at 360 (amb) and 700 (elev) $\text{cm}^3 \text{m}^{-3}$ carbon dioxide concentrations

Variable 1	Variable 2	r	Probability
NCE (elev/amb at 2000)	Acclimation (2000)	-0.797	0.0058
NCE (elev/amb at 500)	NCE (elev/amb at 2000)	-0.142	0.696
Acclimation (500)	Acclimation (2000)	-0.179	0.622

change in RGR with carbon dioxide concentration ($r = +0.068$, $P = 0.851$).

Averaged across species there was no stimulation in RGR by elevated carbon dioxide for the period of 18–24 after emergence, with relative changes ranging from 0.86 to 1.26 (Table 2). The relative change in RGR with carbon dioxide concentration was more strongly correlated with the change in NAR than with the change in LAR (Fig. 2 and Table 3). There was no significant correlation between the changes in NAR and LAR with carbon dioxide concentration (Table 3). The stimulation of NAR by elevated carbon dioxide was positively correlated with the stimulation in NCE measured under the growth conditions (Fig. 3).

Photosynthetic acclimation measured at the growth photon flux ranged from 0.0–2.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 2). The long-term stimulation in NCE at the growth PPFD by elevated carbon dioxide was inversely related to the amount of photosynthetic acclimation (Fig. 4). The amount of photosynthetic acclimation measured at elevated carbon dioxide at the growth PPFD was a good predictor of the response of NAR to elevated carbon dioxide (Fig. 5).

The long-term stimulation of photosynthesis by elevated carbon dioxide measured at high PPFD was also negatively correlated with the amount of photosynthetic acclimation measured at that PPFD (Table 4). However, there was no correlation between the photosynthetic responses to elevated carbon dioxide measured at the two different PPFD's (Table 4), either in terms of net long-term stimulation of photosynthesis or in the amount of photosynthetic acclimation to elevated carbon dioxide.

The cool climate species, as a group, did not differ significantly from the warm climate species in the stimulation in final dry mass, RGR, NAR or NCE, or the amount of photosynthetic acclimation in response to elevated carbon dioxide (Tables 1 and 3, statistics not shown). The weed species, as a group, did not differ from the crop species in these characters (Tables 1 and 3, statistics not shown).

Discussion

The large range of the relative stimulation in mass at the final harvest by elevated carbon dioxide represented only

small differences in the stimulation of RGR over the whole growth interval. The variation in the relative stimulation in dry mass at the final harvest among these species was not correlated with the stimulation of RGR by elevated carbon dioxide. This could occur (mathematically) because of the wide range in initial (seed) mass among species. This data supports the suggestion of Poorter (1993) that differences in the stimulation of biomass by elevated carbon dioxide can result from differences in RGR in ambient air among ecological groups of species, as well as from differences in the stimulation of RGR. The greater relative stimulation in mass by increasing carbon dioxide in species with high RGR may be expected to be quite common among C₃ species since it does not depend on differences in the response of RGR to elevated carbon dioxide, and can even overcome moderate differences in the response of RGR, as in this study. Ecological processes such as competition and carbon sequestration may differ in whether they are more influenced by changes in the relative stimulation of mass or RGR.

Since it was not possible to make leaf gas exchange measurements on very young plants, photosynthesis was compared with growth analysis performed near the end of the growth period.

RGR over this 18–24 d interval was not consistently increased by growth at elevated carbon dioxide across species. It is common for differences in biomass between carbon dioxide treatments to be caused by brief initial differences in RGR (cf. Poorter 1993). Substantial increases and decreases in RGR with elevated carbon dioxide over this interval occurred in the present experiment. The results given here do not fit the pattern observed by Poorter (1993) of greater stimulation in RGR at elevated carbon dioxide in species with greater RGR in ambient air; no significant correlation between these variables was found in this study. Additionally, there were substantial differences among species in the response of NAR to elevated carbon dioxide in this study. It is possible that these differences between our results and those of Poorter (1993) were caused by the lower PPFD used by Poorter limiting the expression of potential differences in photosynthetic response. Among the species examined here, the less acclimation of photosynthesis occurred at elevated

carbon dioxide, the greater was the stimulation of photosynthesis and NAR in the growth environment. Differences in self-shading effects on NAR between carbon dioxide treatments would tend to obscure the correlations between the stimulation of NCE and of NAR. The high correlation between the stimulation of NCE and of NAR by elevated carbon dioxide indicates that differences in self-shading did not substantially confound the results. The response of RGR was positively correlated with the response of NAR. The data suggests that species differences in photosynthetic acclimation to elevated carbon dioxide may be an important factor in determining how RGR would respond to increasing carbon dioxide. It is not possible with the present data to determine how much species differences in photosynthesis affected earlier responses of RGR to elevated carbon dioxide.

As a cautionary note, photosynthetic response and acclimation to elevated carbon dioxide differed depending on the PPFD used to measure photosynthesis. This could greatly complicate predictions of the relative stimulation of NAR by elevated carbon dioxide in variable PPFD environments. In soybean, reduced photosynthesis after acclimation to elevated carbon dioxide assayed at high PPFD was accompanied by a reduction in the quantum yield of photosynthesis (Sicher *et al.* 1996), but this may not be true in all species, or at least apparently

not to the same extent. Understanding relationships between acclimation to elevated carbon dioxide of photosynthesis measured at high and low PPFD will be important to predictions of photosynthesis as atmospheric carbon dioxide increases.

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